Noteworthy anatomical and physiological researches.

Some recent cell literature.

The literature of the various problems touched by studies on the cell increases so rapidly and leads so often to modifications in our knowledge and our theories of cell-phenomena, that the best hand-book very quickly becomes antiquated, perhaps more quickly at present in this field of research than in any other. It is now little more than two years since the appearance of Hertwig's admirable summary of our cytological knowledge, "Die Zelle und die Gewebe," but already certain disputed points there discussed have been further elucidated, and certain views there defended have gained or lost in probability. The request of the editors of the GAZETTE for a brief account of recent literature in its effects on our knowledge of the nucleus and centrospheres seems therefore justifiable. In this discussion we may best take Hertwig's book as a starting point; for, although it treats the cell from the stand-point of the animal histologist, it shows the thorough acquaintance of its author with the botanical literature and his willingness to use it wherever it can throw light on the problems discussed. The present account will, naturally, deal chiefly with the literature of the plant-cell, while referring also to certain important zoological papers.

The question of the nature of the nucleoli and of their fate during karyokinesis is still an open one. While Strasburger and others believe that the substance of these bodies becomes dissolved in the so-called nuclear sap, it is pretty generally held by zoologists to be taken up by the chromosomes. The position taken by Moll (12) may be regarded as an extreme form of this view. He finds in the resting nucleus of *Spirogyra* a very large nucleolus which gradually disappears as the chromatin thread becomes more prominent during the spirem stages. And he believes that he has observed the termination of one end of this thread in the nucleolus, which thus directly furnishes the material for the formation of the chromosomes. Only further studies can definitely decide this important question which bears so directly on the nature of the nucleoli. Zimmerman (20) has observed, like others be-

fore him, that masses of nucleolar substance may sometimes be seen in the cytoplasm during karyokinesis. But this author attempts to show that the nucleoli are characteristically thrown out of the mother-nucleus into the cytoplasm during division, to be reabsorbed into the daughter-nuclei. The present reviewer (9) has attempted to show that this extrusion of nucleolar substance is not constant, nor even common, in any plant studied by him; and Guignard has found (7) in *Psilotum triquetrum* that the frequence of the phenomenon depends, in the sporogenous tissue, upon the stage of its development. The writer can see nothing in the behavior of nucleoli to justify Zimmerman's view of them as organs of the cell. Their indefiniteness in form, size, number, and position in the nucleus, and their total disappearance in most cases during karyokinesis, all point to the conclusion that they are masses of substance subject to the activity of the nucleus and perhaps furnishing plastic material for certain cell-processes, to whatever parts of the cell it may be distributed while unrecognizable as nucleolar masses. And the fact that such recognizable masses sometimes occur in the cytoplasm affords no evidence that the whole of this substance passes normally into the cytoplasm when it disappears during karyokinesis. It is perhaps quite as probable that these masses represent a surplus which is not or cannot be disposed of in the usual way.

The observation of nucleolar masses in the cytoplasm in *Psilotum triquetrum* led Karsten (10) to believe that they are the centrospheres, and that therefore, at least in this plant, the latter bodies are of nucleolar origin. The writer (9) has shown that this was due to his having quite overlooked the true centrospheres, a conclusion since entirely confirmed by Guignard (7).

Since their first discovery in plant-cells by Guignard, the centrospheres have been recognized with more or less certainty by various investigators, so that their occurrence in most of the great groups of plants seems now assured. As has been intimated, the evidence is not equally satisfactory in all cases that the structures regarded as centrospheres by the various writers have really been such. But, as it is practically impossible to determine justly the merits of each case, it may suffice to give a systematic list of those plants in which they are claimed to have been seen, with the name of the observer in each case.

ALGÆ: *Surirella calcarata*, Bütschli, (2); Lauterborn, (11).
Pinnularia nobilis Bütschli, (3).
Spirogyra sp., de Wildeman, (18).
Chara fœtida, Schottländer, (14).
Sphacelaria scoparia, Strasburger, (15); Humphrey, (9).
FUNGI: *Agaricus galericulatus*, Wager, (17).
BRYOPHYTA: *Marchantia polymorpha*, Schottländer, (14).
Pellia epiphylla, Farmer and Reeves, (5).
PTERIDOPHYTA: *Gymnogramme* sp., Schottländer, (14.)
Asplenium sp., Guignard, 1891.
Polypodium sp., Guignard, 1891.
Osmunda regalis, Humphrey, (9).
Equisetum limosum, de Wildeman, (18).
Psilotum triquetrum, Humphrey, (9); Guignard, (7).
Isoetes sp., Guignard, 1891.
GYMNOSPERMAE: *Ceratozamia longifolia*, Humphrey, (9).
ANGIOSPERMAE: *Liliaceæ* (*Lilium*, *Fritillaria*, *Allium*), Guignard, 1891; Schaffner, (13).
Amaryllidaceæ, *Orchidaceæ*, etc. Guignard, 1891.
Tradescantia sp., Guignard, 1891.
Vicia Faba, Schaffner (13).

The fact that they have been seen chiefly in the reproductive cells is due plainly to the greater size and better development of most important structures in such cells. But there is no reason to doubt their occurrence in purely vegetative cells also. Their minute size and the difficulty with which they take up stains makes their recognition in most plants dependent on very favorable conditions for observation. But in some algæ, including some diatoms, according to Bütschli, they are much more easily recognizable, even in the living cell.

In his cell-book Hertwig inclines to the view that these bodies will be found to be of nuclear, rather than of cytoplasmic origin. But the results of the past two years do not, on the whole, favor this opinion. Certain zoologists, notably Brauer (1), believe they have observed them within the nucleus before division, but botanical workers on this point, with the exception of Karsten, agree in finding them in the cytoplasm during the resting stage, in agreement with the original observations of Guignard. Reference may be had to papers by Strasburger (15), Humphrey (9), Guignard (7),

and Schaffner (13). Karsten's theory (10) of the derivation of the centrospheres from the nucleoli has been shared by Julin and other zoologists; but the source of his error has already been pointed out, and the observations of most students of animal cells are equally opposed to this view.

As early as 1888, Boveri gave the name *archoplasm* to the centrosomes with the surrounding cytoplasm, and this term has been more or less loosely used by subsequent writers. Strasburger has more recently (15) proposed to distinguish that part of the cytoplasm which appears to play an active part in karyokinesis, surrounding and including the centrosomes, as *kinoplasm*, from the merely nutrient portion, or *trophoplasm*. And this distinction is a very useful one. In their morphological application, the terms archoplasm and kinoplasm appear to be synonymous. The number of centrosomes present in the kinoplasm of a cell just before division appears to be typically two. In animals and in some algæ the number during the resting stage is but one, and this divides as a preliminary to nuclear division. In the higher plants this division occurs before the resting period, and indeed in the earliest stages of the formation of the daughter nucleus which the kinoplasm accompanies. Heidenhain (8) finds in some animal cells as many as a hundred granules in a group, which he regards as equivalent to a single center. But it seems fair to ask if these may not represent pathological conditions or artificial products. At all events, no such condition has been recognized in plants.

Normal karyokinesis appears to be introduced by the passage to each pole of the nucleus of a part of the kinoplasm with a centrosome, and by the formation, apparently from these starting points, of a spindle-shaped frame-work of delicate fibres. The question as to the source from which the material of these fibres is derived has long been a matter of dispute. Most zoological writers have believed it to be formed chiefly within the nucleus, while most botanists maintain for it an extra-nuclear origin. Flemming now concedes that the ends of the spindle originate outside of the nucleus, while Hermann and the latest writer on karyokinesis in animals, Drüner (4), fully agree with Strasburger in deriving it from the kinoplasm.

The disagreement among zoologists as to whether the spindle

fibres are continuous from pole to pole was due to insufficient knowledge of the facts. The difficulty has been cleared up by the pretty general acceptance of the view that there are formed in some cells, such as the spermatocytes of the salamander, continuous spindle-fibres reaching from pole to pole, and, outside of these, groups of peripheral fibres which reach, at farthest, only to the equator of the spindle; while in other cells, including the egg of *Ascaris megalocephala*, only these peripheral fibres, and none of the central spindle, appear to be formed. Hermann and Drüner derive the central spindle, where it has been observed, from the substance connecting the centrosomes. It appears at first very small and grows as the centrosomes separate. A somewhat similar phenomenon is described by Lauterborn (11) as giving rise to a spindle-like structure in one of the diatoms. This observation needs confirmation, but points to processes of much interest. Strasburger (16) denies the existence of peripheral fibres in the higher plants and finds the threads of the spindle always continuous. Therefore, until our knowledge of facts is much more complete, it is useless to discuss the homologies and significance of the structures above mentioned.

It is, perhaps, in their ideas of the mechanics of the karyokinetic process that vegetable and animal cytologists remain still most widely apart. Most zoologists regard the arrangement of the chromosomes into an equatorial plate and the migration of the daughter-chromosomes to the poles of the spindle as the direct result of the active growth and subsequent retraction of the peripheral fibres. These are believed to grow outward from the centrosomes, attaching themselves to the chromosomes and pushing these before them until they reach the equator, where fibres from opposite poles become attached to the respective halves of each chromosome. Now begins the contraction of the fibres, which results in the separation of the daughter-chromosomes and in their being drawn finally to the poles, on the complete retraction of the peripheral fibres. Drüner (4) also attributes the migration of the centrosomes to the poles of the nucleus to the push of the fibres seen radiating from them at this time, against cell-wall and nucleus, their paths being determined by the resultants of all the pushes to which they are exposed. Many zoologists, with this writer, regard the centrosomes as mere points of attachment for the kinoplasmic threads.

On the other hand, as has been said, Strasburger (16) denies the existence of peripheral fibres in the best-studied plants. Maintaining justly that the splitting of the chromosomes is an active, vital phenomenon, he holds that the movement of the daughter chromosomes to the poles is equally so. He considers the spindle fibres to be the guiding paths along which the chromosomes move, since he and Guignard have found a close correspondence in number between these fibres and the chromosomes. And he believes their motion to take place in response to some sort of attraction exerted by the centrosomes. Yet, since all radiations from the centrosomes are so faintly visible in plant-cells treated by the best known methods, Flemming's suggestion (6) is worthy of consideration, when he hints that an improved technique may bring out the peripheral fibres in these cells, also.

Of the details of karyokinesis in most of the *Thallophyta* we know very little, and most of the accounts we possess contain details so at variance with what we know of other groups, that they must be regarded as requiring confirmation. This seems especially true of the accounts of the centrosomes in these plants which have been published.

Concerning the process of cell-fusion, which constitutes the essential feature of fertilization, there have been no very recent advances on the vegetable side; but it should be noted that recent studies of some American zoologists (19) tend strongly to discredit the supposed fusion in pairs or "quadrille" of male with female centrosomes. The centrosomes of the fertilized egg are said to be furnished sometimes by one, and sometimes by the other sexual element. If this be true for animals, a similar condition may be expected among plants also; but, until Guignard's observations of the quadrille in *Lilium Martagon* are proved erroneous, there is no ground for doubting their accuracy.

Since the present status of our knowledge of the facts concerning the reduction of the number of the chromosomes in the nuclei of the gametophyte, and of their significance so far as plants are concerned, has lately been sketched in this journal (**20:** 23), in an abstract of Strasburger's last paper, it will not be profitable to discuss that most interesting cytological phenomenon here.—J. E. HUMPHREY.

PAPERS REFERRED TO.

1. BRAUER, A., Zur Kenntniss der Spermatogenese von Ascaris megalocephala. Arch. f. micr. Anat. **42**: 197. 1893.
2. BUETSCHLI, O., Ueber die sog. Centralkörper der Zelle und ihre Bedeutung. Verhandl. des naturh.-med. Vereins zu Heidelberg **4**: 535. 1891.
3. BUETSCHLI, O., Ueber die Bewegung der Diatomeen. Loc. cit. **4**: 580. 1892.
4. DRUENER, L., Studien über Mechanismus der Zelltheilung. Jena. Zeitsch. für Naturwiss. **29**: 271. 1894.
5. FARMER, J. B. and REEVES, J., On the occurrence of centrospheres in Pellia epiphylla, Nees. Annals of Botany **8**: 219. 1894.
6. FLEMMING, W., Zelle, in Merkel und Bonnet, Anatomische Hefte **3**: 113. 1894.
7. GUIGNARD, L., Sur l'origine des sphères directrices. Journ. de Botanique **8**: 241. 1894.
8. HEIDENHAIN, M., Neue Untersuchungen über die Centralkörper und ihre Beziehungen zum Kern- und Zellenprotoplasma. Arch. für micr. Anat. **43**: 423. 1894.
9. HUMPHREY, J. E., Nucleolen und Centrosomen. Ber. d. deutschen bot. Gesell. **12**: 108. 1894.
10. KARSTEN, G., Ueber Beziehungen der Nucleolen zu den Centrosomen bei Psilotum triquetrum. Ber. d. deutschen bot. Gesellsch. **11**: 555. 1893.
11. LAUTERBORN, R., Ueber Bau und Kerntheilung der Diatomeen. Verhandl. des naturhist.-med. Vereins zu Heidelberg **5**: 112. 1893.
12. MOLL, J. W., Observations on karyokinesis in Spirogyra. Verhand. d. Kon. Akad. d. Wetensch. te Amsterdam **30**:—. 1893. [No. 9.]
13. SCHAFFNER, J. H., The nature and distribution of attraction-spheres and centrosomes in vegetable cells. Bot. Gazette **19**: 445. 1894.
14. SCHOTTLAENDER, P., Beiträge zur Kenntniss des Zellkerns und der Sexualzellen bei Kryptogamen. Beitr. zur Biol. der Pflanzen **6**: 267. 1892.
15. STRASBURGER, E., Schwärmsporen, Gameten, pflanzliche Spermatozoiden, und das Wesen der Befruchtung. Histol. Beiträge 4: 47. 1892.
16. STRASBURGER, E., Zu dem jetzigen Stande der Kern- und Zelltheilungsfragen. Anat. Anzeiger **8**: 177. 1893.
17. WAGER, H., On the presence of centrospheres in Fungi. Annals of Botany **8**: 321. 1894.
18. DE WILDEMAN, E., Sur les sphères attractives dans quelques cellules végétales. Bull. Acad. roy. de Belgique **21**: 594. 1891.
19. WILSON, E. B., and MATTHEWS, A. P., Maturation, fertilization, and polarity in the echinoderm egg. Journ. Morph. **10**: 319. 1895. See also papers in the same number by WHEELER and MEAD.
20. ZIMMERMANN, A., Ueber das Verhalten der Nucleolen während der Karyokinese. Beitr. zur Morph. und Phys. der Pflanzenzelle 2: 1. 1893.